Nitrogen Nutrition and Genotype Interactions in Maize

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Nitrogen (N) is one of the major factors affecting both production efficiency and ground water quality. As the concern over nitrate (NO_3^-) pollution increases, ammonium (NH_4^+) nutrition will undoubtedly become more important for crop production, especially when high efficient nitrification inhibitors are being developed as N management tools. However, there is the misgiving that crops may not perform well under NH_4^+-N. This is a legitimate concern because breeding programs and selections have been conducted under predominantly NO_3^--N environments which might inadvertently eliminate the trait for NH_4^+-N utilization. As a first step towards developing varieties capable of performing under NH_4^+-N, maize is being used as a model system to evaluate the mechanism and efficiency of NH_4^+ assimilation so that a biochemical selection index can be developed for breedin gprograms.

Metabolic Efficiency of NH_4^+ and NO_3^- Nutrition

A deficiency of N is the msot frequent limitation for vegetative growth and grain yield. Thus, maize grain yield responds positively to N fertilizer (Welch, 1979). During the first eight days of development, maize seedlings relay totally on endogenous N in the endosperm to sustain optimum growth (Handa *et al.,* 1985). However, withholding exogenous N longer than 18 days may reduce the rate of subsequent vegetative growth, indicating that an adequate availability of N throughout early growth is critical for maximum nutrient efficiency and plant development (Handa *et al.,* 1985). Although both NO_3^- and NH_4^+ forms of N can be taken up by maize plants, NH_4^+ is absorbed relatively rapidly by roots and utilized more effectively than NO_3^- for protein synthesis (Schrader *et al.,* 1972); and tissue accumulate more N from NH4+ than from NO_3- (Dibb and Welch, 1976 ; Handa *et al.,* 1984; Xu *et al.,* 1992). In addition, NO_3^-absorbed after the mid-silk stage may not be utilized for grain filling (Friedrich *et al.,* 1979; Friedrich and Schrader, 1979), and certain prolific genotypes are not able to take up NO_3^- during grain development (Pan *et al.,* 1984).

Although NH_4^+ may be metabolically efficient and able to enhance sugar movement, a high concentration of NH_4^+ as the only N source could create a "carbon stress" to restrict growth and development. This occurs

because a small accumulation of NH_4^+ in maize tissues may be toxic (Anderson and Done, 1977; Magalhaes *et al.,* 1984). On the other hand NO_3- may accumulate without utilization (Schrader *et al.,* 1972; Chevalier and Schrader, 1977); therefore, the mixture of NO_3- and NH_4+ ions in plants may function as a "fuffer" for optimizing nitrogen utilization. A higher vegetative growth was obtained when maize plants were grown with mixtures of NO_3^--N and NH_4^+-N than with either NH_4^+-N or NO_3^--N alone (Schrader *et al.,* 1972; Handa *et al.,* 1984; Xlu *et al.,* 1992). However, the ability of plants to tolerate a high proportion of N in NH_4^+ form might be concentration and genotype dependent. As shown in Table 1, B73 X Mo17 seedlings preferred a greater proportion of NH_4^+ over NO_3^- when grown under a lower level of N (0.2 mmol); however, as the N level increased, seedling dry weight increased more rapidly with a higher proportion of NO_3-, presumably because of difficulties in full assimilatign high NH_4^+ concentrations. Thus, while NH_4^+ plays an important physiological role in enhancing the movement of sucrose from leaves to vegetative and kernel sinks, and increases photosynthetic activity, nitrate functions as a nitrogen reserve. This "buffering" effect could be especially important during seedling growth when maize plants have only a limited capacity to fix CO_2.

Although NH_4^+-N is the most widely used form of N fertilizer applied for crop production, it may be rapidly nitrified so that most of the soil N available for plant uptake is in the form of NO_3^-. Under this condition, plants not only encounter metabolic inefficiency of NO_3^--N, environment also suffers from a potential contamination. When plants are grown with NO_3^--N source, its reduction in plant tissues appears to be the rate regulating step for N assimilation. Although leaves are the major site of NO_3^- assimilation, some NO_3^- may also be reduced in root tissues (Lea, 1980; Oaks and Hirel, 1985). The first step in NO_3^- assimilation, the reduction of NO_3^- to NO_2^-, is catalyzed by nitrate reductase (NR). Nitrite is then subsequently reduced by nitrite reductase to NH_4^+ before incorporation into organic N. Although reductases from the leaves and roots are apparently different, both are inducible by their substrates (Aslam and Oaks, 1976). Genotypic variation of NR activity which exist (Schrader *et al.,* 1966; Hageman *et al.,* 1976) have not been positively correlated with grain yield (Deckard *et al.,* 1973; Rao *et al.,* 1977).

NH_4^+ Assimilation

The efficiency of NH_4^+ assimilation via the glutamine synthetase (GS)/glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH) systems may be other key regulatory steps in enhancing N utilization and CO_2 assimilation in maize. When maize plants are grown in the presence of a nitrification inhibitor, the level of NH_4^+ may increase substantially - especially during early stages of growth. Unlike NO_3^-, NH_4^+ is relatively toxic at low concentrations in vivo (Masumoto *et al.,* 1971; Anderson and

Table 1. Effects of N form and quantity on dry weight and tissue N concentration of 30-day-old seedlings of B73 X Mo17

N rate (mmol)	N source		Dry weight			N conc.	
	NH_4^+	NO_3^-	Shoot	Root	Total	Shoot	Root
	%		g/seedling			%	
0.2	100	0	1.27	0.70	1.97	1.35	1.26
	75	25	1.33	0.70	2.03	1.42	1.24
	50	50	1.23	0.63	1.86	1.25	1.19
	25	75	1.17	0.63	1.80	1.48	1.27
	0	100	1.07	0.60	1.67	1.36	1.19
1.0	100	0	2.13	0.94	3.07	2.77	1.77
	75	25	2.81	0.91	3.72	2.62	1.63
	50	50	2.91	0.86	3.77	2.57	1.72
	25	75	2.68	0.88	3.56	2.56	1.62
	0	100	2.60	0.88	3.48	2.23	1.49
2.0	100	0	2.76	0.68	3.44	3.96	2.46
	75	25	3.43	0.86	4.29	3.51	2.36
	50	50	3.56	0.88	4.44	3.43	2.12
	25	75	3.30	0.94	4.24	3.38	2.01
	0	100	3.07	1.04	4.11	3.12	1.93
5.0	100	0	2.21	0.62	2.83	4.45	3.31
	75	25	2.86	0.86	3.72	4.38	2.94
	50	50	3.20	0.83	4.03	4.52	2.92
	25	75	3.74	0.98	4.72	4.12	2.87
	0	100	3.22	0.89	4.10	3.85	2.80
LSD(0.05)			0.23	0.23		0.36	0.34

B73 X Mo17 seedlings (3 pot^{-1}) were grown in vermiculite at 25℃ in a controlled climate room with a 16-h photoperiod at 280 μ E sec^{-1} m^{-2}. One week after planting, the seedlings were flushed every other day with 500 ml of modified Hoagland solution (Handa *et al.*, 1985) containing 1, 5, 10, or 25 mM N as $(MH_4)_2SO_4$, KNO_3, or 3:1, 1:1, and 1:3 combinations of NH_4^+-N and NO_3^--N. The pH was adjusted to 6.5 with KOH. Seedlings were harvested 30 days after planting, separated into roots and shoots, and oven-dried at 70℃ to determine dry weight.

Done, 1977) and must be assimi lated immediately in theroot by the reductive amination of an available carb oxylic acid to form an non-toxic amino acid prior to translocation (Ivanko and Ingversen, 1971). The NH_4^+ directly absorbed or available through reduction of NO_3^- is assimilated into organic N either by 1) the reductive amination of α-ketoglutaric acid by GDH to form glutamic acid or 2) by conjugation with glutamic acid to form glutamine by GS. The amide amino group of glutamine is then transferred to α-ketoglutaric acid to form glutamic acid by GOGAT (Miflin and Lea, 1977). Studies on roots using ^{15}N substrate and enzyme inhibitors (Arima and Kumazawa, 1977; Probyn and Lewis, 1979) suggest that the GS/GOGAT system is the predominant pathway for NH_4^+ assimilation. However, based on a determination of NH_4^+ assimilation in vitro and the calculation of organic N accumulated in the shoot after seedling growth on NH_4^+-N, our studies indicate that GS/GOGAT assimilating system alone was not sufficient to account for all of the organic N transported to the shoot (Handa et al.,1985). Thus, one cannot rule out the possibility that GDH may play an important role in NH_4^+ assimiulation in the root, especially when plants are grown under high concentrations of NH_4^+.

The assimilation of NH_4^+ into organic N occupies a unique position in intermediary metabolism as the primary mechanism for coupling N and carbon (C) metabolism. The assimilation of NH_4^+ and subsequent organic N interconversions require organic acids. These carbon skeletons, which are primarily derived from sucrose made via phosphoenolpyruvate carboxylase (PEP carboxyalse) and ribulose-bisphosphate carboxylase (RuBP carboxylase) activities in photosynthesis, must be translocated to root tissues where the majority of NH_4^+ assimilation occurs (Ivanko and Ingversen, 1971; Raven and Smith, 1976). A limitation of essential carbon-substrates during periods of active NH_4^+ assim ilation may be as devastating to plant growth as a deficiency of NH4+ assimilation enzymatic machinery. Higher plants may avoid periods of carbon depletion and NH_4^+ toxicity by either maintaining a large reserve of carbohydrates, or by increasing photosynthetic capacity in response to NH_4^+ nutrition (Givan, 1979). Since maize is a photosynthetically C_4 type plant, CO_2 fixation is highly efficient; however, the accumulation of assimilates in leaf tisseus due to a low sink demand for photosynthate may cause areduction in the rate of photosynthesis (Herold, 1980). The absorption of NH_4^+ creates a physiological pressure and enhances sucrose translocation from leaves to roots to provide energy and essential carbon skeletons for its assimilation. This movement of sucrose from leaves to roots may relieve the inhibition of CO_2 fixation in leaves (Neales and Incoll, 1968). Thus, the rate of photosynthesis in rice (Watanabe and Yoshida, 1970), barley (N'atr, 1975), and wheat (Khan and Tsunoda, 1970) varies in proportion to the amount of N available. Light st imulation of NH_4^+ assimilation into glutamine further indicates a close relationship between N metabolism and photosynthesis (Magalhaes

et al., 1974). Increased photosynthetic efficiency and translocation of sucrose into the vegetative and kernel sinks should promote vegetqative growth and grain yield.

Effects of Inhibiting Nitrification

These observations clearly suggest an important role of NH_4^+ nutrition for maize grain production. Although NH_4^+-N is the most prevalent form of N fertilizer applied for maize, it may be rapidly converted to NO_3^- in the soil because of nitrification. NO_3^- is susceptible to leaching and denitrification losses; therefore, the pre-plant applied N may not be available for plant utilization during the period of grain-fill. N deficiency during grain-fill may result in the early termination of dry matter accumulation due to an extensive proteolysis of leaf proteins including RuBP carboxylase (Tsai *et al.,* 1991).

Our studies with NH_4^+-efficient maize hybrids, B73 X LH51 and GS854, supports this hypothesis and indicates that an experimental nitrification inhibitor XDE474 was very effective in maintining N in the NH_4^+ form in the soil. In the control plot (20.1 g N m^{-2} without a nitrification inhibitor), the RuBP carboxylase activity of both hybrids decreased rapidly as the enzyme was hydrolyzed after 45 days post-pollination (Table 2). This destruction of RuBP carboxylase from leaf tissues during grain-fill resulted in early termination

Table 2. RuBP carboxylase activity in the developing ear leaves of B73 X LH51 and FS854 grown at 20.1 g N m^{-2} with or without 0.05 g m^{-2} XDE474

Hybrid	XDE474	Days post-pollination				
		40	45	50	55	60
		Activity (μ mol CO_2 g^{-1} fresh weight min^{-1})				
B73 x LH51	None	0.35±0.04	0.24±0.03	0.13±0.01	0.03±0.01	0
	XDE474	0.30±0.04	0.25±0.04	0.16±0.01	0.18±0.02	0.02±0.01
FS854	None	0.22±0.02	0.18±0.01	0.17±0.01	0.04±0.01	0
	XDE474	0.20±0.02	0.22±0.03	0.26±0.03	0.22±0.02	0.04±0.01

Ear leaves of B73 X LH51 and FS854 were collected at 40, 45, 50, 55, and 60 days after pollination. Four ear leaves from each sampling stage were frozen in liquid N immediately after colloection and stored at -80℃ before enzyme extraction. RuBP carboxylase activity was determined in 200 μ l of a reaction mixture containing 100 mM Tricine buffer (pH 8.2), 25 mM $MgCl_2$, 5 mM ribulose 1,5-diphosphate, 10 mM $NaH^{14}CO_3$ (3.7 X 10^4 Bq), and 50 μ l of leaf extract (Evans and Seemann, 1984).

of dry matter accumulation and prevented a further increase in kernel weight and grain yield (Tsai *et al.*, 1991). However, RuBP carboxylase activity in ear leaves of both hybrids was maintained up to 55 days post-pollination when the applied N was stabilized with XDE474 (Table 2). This observation is consistent with the notion that NH_4^+ nutrition is not only metabolic efficient but also important for late season uptake to sustain phososynthetic activity to increase grain yield.

In addition to hydrolysis of enzymes in leaves, nuytrients in the stalk might be cannibalized to support kernel development when plants were grown under Nstress conditions. Our previous studies have suggested that stalk lodging may be, in part, induced by N deficiency in the soil which, in turn, caused a severe cannibalization of nutrients from the stalk to enhance kernel development (Huber *et al.*, 1986). To study the relationship between cannibal ization of nutrientsin the stalk and lodging severity, ear and stalk tissues were separated and airdried to determine dry weight. Results presented in Table 3 are expressed as the dry weight ratio (g/g) of stalk/ear (S/E); thus, the lower the ratio the lighter the stalk (a reflection of more severe can nibalization in nutrients). As expected, lodged plants had a lower S/E ratio than standing plants for these two hybrids studied. This observation is consistent with the hypothesis that lodgingis related to a severe cannibaliza tion of nutrients in the stalk. It is interesting to note that all lodged

Table 3. Dry weight ratio of stalk to ear at maturity of B73 X LH51 and FS854 grown a t 20.1 g N m^{-2} with or without 0.05 g m^{-2} XDE474

Hybrid	XDE474	Standing plants			Lodged plants		
		Stalk	Ear	Stalk/Ear	Stalk	Ear	Stalk/Ear [1]
		--- g $plant^{-1}$ ---		Ratio	---- g $plant^{-1}$ ---		Ratio
B73 x LH51	---	61	234	0. 26	34	175	0. 19
	0. 05	68	272	0. 25	39	195	0. 20
FS854	---	36	217	0. 17	29	204	0. 14
	0. 05	39	216	0. 18	30	214	0. 14

Four lodged and four standing plants from each of the four replicated plots (fertilized with 20.1 g N m^{-2} treated with or without XDE474) were collected. Ears and stalk tissues were separated and air dried at 40℃ before dry weight was determined.

[1] LSD(0.05) between hybrid = 0.067; LSD(0.05) between treatment (with or without XDE474) = 0.055; LSD(0.05) between plant type = 0.062.

plants were consistently smaller than standing plants, thus suggesting the importance of healthy vegetation growth for high yield and better stalk quality. Treatments with XDE 474, although did not improve the S/E value, imcreased dry mass both in the stalk and ears. From the two hybrids evaluated, the S/E ratio for the standing plants was lower with FS854 than that of the B73 X LH51. These observations of nutrient interactions and hybrid variations in affecting S/E ratios agree with the lodging severity of FS854 (unpublished data).

Biochemical Traits of NH^{4+} Assimilation

As the concern over NO_3^- contamination of ground water increases, NH_4^+ nutrition could become more important for crop production, especially when highly efficient nitrification inhibitors are being developed to optimize N management. However, in spite of the high efficiency of NH_4^+ nutrition for crop production, there is the misgiving taht most maize hybrids may not perform well under NH_4^+-N. This is a legitimate concern because breeding programs and selection have been conducted under predominantly NO_3^--N envbironments which might have inadvertently eliminated the trait for efficient NH_4^+ utilization. Therefore, as a first step towards developing maize hybrids capable of performing under NH_4^+-N, maize inbreds were evaluated for the efficiency of NH_4^+ assimilation.

A previous study has shown that 10 mM NH_4^+ provides a near optimum N condition for seedling development (Xu *et al.,* 1992). Therefore, maize inbreds were grown at 10 mM and a high concentration of 50 mM NH_4^+-N to evaluate for their sensitivities of seedling growth to NH_4^+ nutrition. Of the 41 inbred lines screened, only two inbreds grew vigorously with 50 mM NH_4^+-N (more than 70% dry weight of the 10 mM control). thirty -two inbreds grew very poorly with 50 mM NH_4^+ as the only source of N (less than 33% of the 10 mM control).

Va26, A661, H95, Hi31, Pi6875-370, ICAL210, PH9, CI66, A632, TA85-17, and Pi 77-4239, which represent different degrees of sensitivity to NH_4^+-N, were selected for further growthanalysis under mixtures of NH_4^+-N and NO_3^--N. With the exception of A661, all other 10 inbreds studied preferred a high proportion of N in the NO_3^- form (66% or 100% NO_3^--N)(Table 4). These observations are expected because of breeding programs and selection under predominantly NO_3^- environments which might have inadvertently eliminated the trait for efficient NH_4^+ utilization. The finding that certain inbreds such as A661 could tolerate high proportion of N in NH_4^+ form for growth is important for developing maize hybrids which can capitalize on the efficiency of NH_4^+-N for high yield production and thereby permit the greater use of management practices, such as inhibiting nitrification, to minimize potential NO_3^- pollution.

Because NH_4^+ assimilation involved three components: organic carbon skeletons (derived from PEP and RuBP carboxylase activities), assimilating enzymes (GDH, GS,

Table 4. The effect of N forms (30 mM) on total seedling dry matter accumulation in 11 maize inbreds

Inbred	NH_4^+ (mM)/NO_3^- (mM)			
	30/0	20/10	10/20	0/30
	g/seedling			
Va26	0.76	1.07	1.23	1.21
Pi6875-370	1.46	1.75	2.15	1.70
CI66	0.99	1.42	1.79	1.75
H95	1.39	1.66	2.22	1.94
A661	1.28	2.23	2.06	1.94
PH9	0.73	0.86	1.06	1.09
A632	0.92	0.98	1.29	1.20
Hi31	0.62	1.17	1.14	1.49
Pi77-4239	0.60	1.07	1.15	1.63
TA85-17	0.39	0.65	0.83	0.81
ICAL210	0.63	0.95	1.20	1.21

Seedlings (3 pot^{-1}) were grown in sand in a greenhouse. One week after planting, seedlings were thinned so that each pot contained only one seedling of uniform size. Subsequently, each pot was flushed every day with 500 ml of modified Hoagland solution (Handa et al., 1985) containing 30 mM of N as $(NH_4)_2SO_4$, KNO_3, or their mixtures in a ratio of 2:1, or 1:2. The pH was adjusteds to 6.5 with KOH. Seedlings were harvested two weeks after watering with the modified Hoagland solution, separated into roots and shoots, and oven-dried at 70℃ to determine dry weight. The experimental design was randomized complete block arranged in a split-plot with four replications. Conc. LSD(0.05) = 0.08, LSD(0.01) = 0.11; Inbred LSD(0.05) = 0.21, LSD(0.01) = 0.28.

and GOGAT), and NH_4^+ uptkake, efforts were made to determine which components are responsible for the ability or inability of maize inbreds to utilize NH_4^+ nutrition. As shown in Table 5, the correlation coefficient between dry weight accumulation and the activity of GS (r^2= 0.09), GOGAT (r^2= 0.004), GDH (r^2=0.016), or PEP carboxylase (r^2= 0.24) among the 11 inbreds studied was very low. Likewise, there was no correlation between dry weight and NH4+ uptake (r^2= 0.05, Table 6). From these data, it is clear that no one component is entirely responsible for enhanced seedling growth with high NH_4^+ levels and that a more complex interaction between enzymes exists. In owther

words, certain inbred linesretain the ability to effectively utilize ammonium, but adapt various combinations of mechanisms to cope with NH_4^+ pressure and thereby allow seedling growth and development in the presence of NH_4^+ in high concentrations. Therefore, plant breeders should be able to exploit this variability and create hyvrids with enhanced performance under predominantly H_4^+-N conditions. A preliminary study with maize hybrid Tainan 17 and its inbred parents supports this hypothesis.

Table 5. Relationship between seedling dry weight and enzyme activity of NH_4^+ assimilation and PEP carboxylase in 11 maize inbreds

Genotype	Dry weight	GS	GOGAT	GDH	PEPcase
	g/seedling	----------	unit/mg protein/min		----------
Va26	0.84	0.67	0.018	0.015	0.29
Pi6875-370	0.66	0.93	0.038	0.021	0.19
CI66	0.64	0.83	0.073	0.032	0.55
H95	0.52	1.30	0.071	0.021	0.39
A661	0.51	0.83	0.018	0.036	0.35
PH9	0.51	0.52	0.021	0.019	0.65
A632	0.43	0.97	0.049	0.034	0.22
Hi31	0.37	0.33	0.051	0.026	0.64
Pi77-4239	0.34	0.24	0.040	0.023	----
TA85-17	0.30	0.67	0.009	0.028	0.51
ICAL210	0.30	0.44	0.050	0.031	0.49

Three seedlings were grown in sand a growth chamber with a 16-h photoperiod. Two weeks after planting, each pot was water every other day with modified Hoagland solution (Handa *et al.*, 1985) containing 50 mM of N as $(NH_4)_2SO_4$. One week after water with the modified Hoagland solution, seedlings were harvested, and separated into roots and shoots. The harvested samples were divided into two lots: one lot was placed in an oven at 70℃ for dry weight determinations. Root and shoot tissues in the second lot were washed, blotted, weighed, and frozen in liquid nitrogen before determining the activity of enzymes. GDH was assayed in the aminating direction by a modified method of Wallace (1973). GOGAT was assayed using a modified method of Dougall (1974). GS activity was assayed using a modification of the method of Kanamori and Matsumoto (1972). PEP carboxylase was assayed using a modification of the method of Podestra and Andreo (1989). Unit for GS is μ moles γ -glutamyl-hydroxamate formed; unit for GOGAT, GDH, and PEPcase is μ moles NADH oxidized.

Table 6. Relationship between NH uptake activity and seedling dry weight of 11 maize inbreds

Genotype	Dry weight	Uptake
	g/seedling	μ mol/g FW/h
Va26	0. 84	2. 25
Pi6875-370	0. 66	2. 30
CI66	0. 64	1. 43
H95	0. 52	1. 45
A661	0. 51	4. 25
PH9	0. 51	2. 67
A632	0. 43	1. 26
Hi31	0. 37	2. 90
Pi77-4239	0. 34	1. 64
TA85-17	0. 30	1. 56
ICAL210	0. 30	0. 31

Seedlings were grown in sand in a growth chamber with a 16-h photoperiod. Two weeks after planting, each pot was watered every other day with modified Hoagland solution (Handa *et al.*, 1985) containing zero N. One week later, seedlings were harvested for measuring the uptake of NH_4^+ ions using the method described by Topa and Jackson (1988).

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玉米利用不同氮態肥的反應及策略

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氮肥是影響作物生產與環境的重要因素，由於社會對於環境污染的關切，今後的作物生產將得借重於目前開發中的第二代硝化抑制劑以減輕硝態氮的污染。銨態氮雖然不致於污染環境，而且理論上它的代謝效率也高，但是一般作物都難以適應較高濃度的銨態氮。這是由於長年的育種工作都在硝態氮環境下進行，導致絕大部分品種利用銨離子之遺傳特性的遺失。爲了因應未來的銨態氮生產方式以減輕硝態氮對於環境的污染，乃以玉米爲模示探討品種間對於銨態氮的利用能力，尋求生化指標做爲今後育種善於利用銨態氮雜交品種的依據，以解決作物生產力與環境污染的衝突。